LEACHING AND DECOMPOSITION OF MOUNTAIN BEECH LITTER (*NOTHOFAGUS SOLANDRI* : FAGACEAE) IN A MOUNTAIN STREAM

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SUMMARY: Results of field and laboratory experiments on decomposition of leaves and twigs of mountain beech *(Nothofagus solandri* var. *cliffortioides)* submerged in stream water are presented. Litter released up to 6% of its initial dry weight as leachate within 11 days of immersion. Subsequent losses of water soluble components from litter were constant at about 0.05% per day. Litter in 0.2 and 1.0 mm mesh bags kept in a mountain stream lost up to 65% of initial dry weight in one year. This loss rate is slower than that of any litter species reported to date but was partly due to the inclusion of twigs in the present study. Macrofauna colonising the bags did not affect weight loss. Nitrogen increases of up to 0.5% in litter are attributed to microbial colonisation. Although weight losses conformed to linear, positive and negative exponential, and logistic models, consideration of possible mechanisms of weight loss suggests that the latter represents the most accurate interpretation.

INTRODUCTION

Small forested streams are predominantly heterotrophic (Fisher and Likens, 1972, 1973; Sedell *et al.,* 1974; McDowell and Fisher, 1976; Fisher, 1977) and it is now generally accepted that, in such streams, consumers depend heavily on allochthonous inputs of dead leaves and other terrestrial debris (Cummins, 1974). Decomposition is the main process involved in the release of energy contained in organic matter in streams (Saunders, 1976) but rates vary considerably and are affected by many factors (Peterson and Cummins, 1974; Reice, 1974). Most decomposition is biologically mediated (Saunders, 1976) although physiocochemical processes such as photo-oxidation and leaching also occur. Biological decomposition results mainly from microbiological processes (Triska, 1970; Barlocher and Kendrick, 1974) although, in many small forested streams, macroconsumers may signicantly affect rates of weight loss from organic debris (Cummins *et al.,* 1973).

In New Zealand, two varieties of a small leaved beech *(Nothofagus solandri)* form extensive evergreen forests, especially on the eastern slopes of the main divide in the South Island where they are often the only canopy tree species present (Wardle, 1970). Forests dominated by this species have been extensively studied in New Zealand (Wardle, 1970; Bagnall, 1972; New Zealand Ecological Society Symposium, 1974) although few studies have been made of associated stream ecosystems. Some recent work on beech forest streams has investigated the role of litter in energy flow (Winterbourn, 1976; Davis and Winterbourn, 1977; McCammon, 1978) and the biology of benthic invertebrates (Winterbourn and Davis 1976; Winterbourn, 1978). The present paper reports on the leaching and decomposition of mountain beech litter and forms part of this wider study.

THE STUDY AREA

Field work was carried out in Middle Bush stream, a small stream which flows through an isolated stand of mountain beech *(N. solandri* var. *cliffortioides* (Hook. f.) Poole) at Cass (600-700 m a.s.l.), on the eastern slopes of the Southern Alps (43°02' South, 171°46' East). The forested section of the stream has a rugged bed less than 2 m wide and comprises a stepped series of riffles and pools with several small waterfalls usually less than 1 m high. Mountain beech litter enters the stream throughout the year (Winterbourn, 1976) and, at times, large accumulations of leaves and twigs may be found in pools or tangled in jams formed from branches and other debris.

Stream discharge, measured semi-continuously at a v-notch weir from September 1973 to July 1974, averaged 5 *l*/sec and ranged from less than 1 *l*/sec to about 50 *l*/sec. Water temperature during the same period ranged from 0.0-14.0°C. Stream water is moderately soft (total alkalinity 0.56-0.75 meq / *l*)

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and has a pH of 6.7-7.1. A detailed description of the stream and catchment is given by Winterbourn and Davis (1976).

METHODS

1. *Leaching experiments*

Leaves and twigs of mountain beech were collected from three sources: living material was taken from trees near the stream, newly fallen litter was collected in litter-fall traps placed around the margins of the stream, and water-soaked litter was collected from the stream bed. Material was dried at 70 °C to constant weight and about 10 g quantities were weighed to the nearest 10 mg. Samples were placed into tubular PVC containers, which were then closed with 1.0 mm mesh netting and left in a laboratory channel containing continuously circulating water from Middle Bush stream. Water temperature was kept at 6-8 °C. To minimise microbial activity on litter samples, full spectrum antibiotics were added to the water each week according to the method outlined by Kaushik and Hynes (1968). Triplicate samples were removed from the channel after one, five, and 11 days and thereafter at about 20-day intervals for two months.

2. *Decomposition studies*

Newly fallen litter was collected from Middle Bush and dried at 70 °C to constant weight. Accurately weighed samples of about 10 g (about 1:1 (w / w) leaves to twigs) were sewn into flat nylon mesh bags (100 X 150 mm). Mesh sizes 0.2 and 1.0 mm were used to allow differential colonisation by microflora and macrofauna. Series of three bags of each mesh size were sewn into 12 large 10 mm mesh nylon sacks and anchored in the stream in July 1973. One sack was removed from the stream after two weeks and the remainder at about monthly intervals. After removal, litter samples were washed gently in a 1.0 mm mesh Endecott sieve and any macrofauna were removed and stored in 70% alcohol. Litter samples were dried at 70 °C, weighed and later macerated in a Waring blender. Nitrogen content of macerated litter samples was determined from three sub-samples using Maciolek's (1962) modification of Conway's (1958) micro-diffusion method.

RESULTS AND DISCUSSION

1. *Leaching experiments*

Rapid weight losses from living material and newly fallen litter occurred during the first 11 days and were followed by a period of slower and constant weight loss (Fig. 1). In contrast, litter from the stream bed showed rapid leaching for only one day. This partitioning of leaching weight losses into an initial rapid and later slow phase is similar to results obtained by other workers (e.g., Nykvist, 1963; Petersen and Cummins, 1974) although the time over which rapid weight losses occurred was 5-10 times longer than those reported for leaves of most northern hemisphere species. Each litter type lost about 1.5 % of initial weight after one day, but after 11 days newly fallen litter had lost 4.5 % of initial weight whereas living material had lost almost 6 %. These values are comparable with those found for leaves of several northern hemisphere species of Fagaceae (Petersen and Cummins, 1974; McDowell and Fisher, 1976). Differences in the amounts leached from each litter type probably results from chemical differences. Newly fallen litter is likely to contain a smaller amount of water soluble substances than living material since many organic components of leaves are broken down

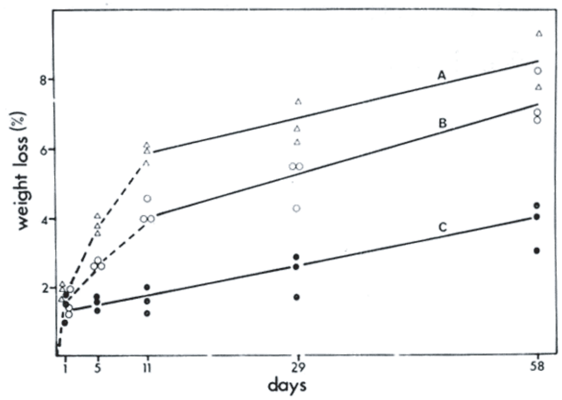

FIGURE 1. *Leaching from mountain beech litter in a laboratory channel. Solid lines fitted by least squares regression (see Table* 1). *broken lines fitted by eye.* A = *living material;* B = *newly fallen litter;* C = *litter collected from the stream bed.*

TABLE 1. *Least squares regression equations for the slow (second) phase of leaching from mountain beech litter in a laboratory channel (see Figure 1).*

Litter Type	Equation	F-ratio
Living material	% L = 5.21 + 0.056.t	24.5*
Newly fallen litter	% L = 3.33 + 0.067.t	42.8*
Stream litter	% L = 1.24 + 0.042.t	53.8*

* = $p < 0.01$.

and resorbed during leaf senescence (Wareing and Phillips, 1970). Litter from the stream bed presumably had lost most of its readily available water soluble component through previous leaching in the stream. However, Nykvist (1963) has shown that additional weight losses may occur if previously leached material is dried and releached.

Analysis of covariance of weight loss data from the second slow phase of leaching showed that loss rates of the litter types did not differ significantly after the initial rapid leaching had occurred. Weight losses during this latter period showed significant fits to linear regressions (Table 1) and assumed a constant rate of about 0.05 % of initial weight per day.

2. *Decomposition studies*

Changes in dry weight of litter kept in coarse and fine mesh bags in the stream are shown in Figure 2. About 60 % of initial dry weight was lost after one year, a loss rate slower than that reported for any leaf species including some northern Fagaceae assigned to the "slow breakdown" group of Petersen and Cummins (1974). The biological half life (t_{50}) of decomposing mountain beech litter estimated in the present study was about 300 days, whereas Davis and Winterbourn (1977) found a t_{50} of about 150 days for mountain beech leaves (as opposed to leaves and twigs) in the same stream.

Previous studies of litter decomposition in streams (see references in Petersen and Cummins, 1974) have determined weight loss from leaves only, whereas litter used in the present study included about 50 % twigs. Weight loss from twigs is likely to be slower than from leaves (Boling *et al.*, 1975; Saunders, 1976) because twigs are highly lignified and may not be readily decomposed or eaten by consumers (Triska, Sedell and Buckley, 1975). For this reason, and because a complex of other variables affect litter breakdown rates (Park, 1974; Reice, 1974) direct comparisons with other studies are of limited value.

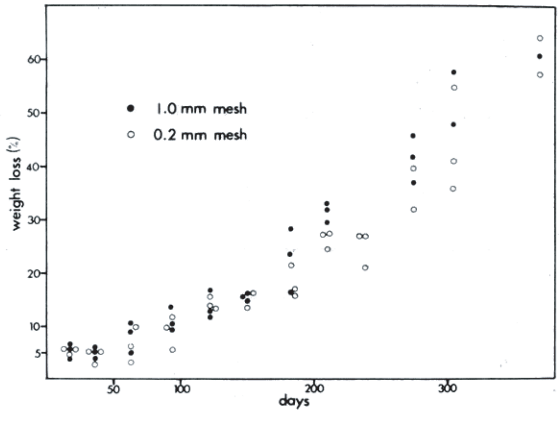

FIGURE 2. *Weight loss from mountain beech litter kept in mesh bags in the stream.*

Several authors have shown that stream invertebrates may influence weight losses from litter. Cummins *et al.* (1973) found that the presence of large particle detritivores (shredders) doubled weight losses from hickory *(Carya glabra)* leaves although no such increases were noted for oak *(Quercus* spp.) leaves. Davis and Winterbourn (1977) found that mountain beech leaves in 1.0 mm mesh bags were colonised by stream invertebrates. Larvae of the trichopterans *Zelandopsyche ingens* and *Olinga jeanae* and the plecopteran *Austoperla cyrene* were the only important shredders colonising their bags and, along with helodid larvae (Coleoptera) and a small stonefly *Spaniocerca zealandica,* were considered to be at least partially responsible for weight losses from the leaves.

In the present study, numbers of larger invertebrates colonising 1.0 mm mesh bags were similar to those found by Davis and Winterbourn (1977) (Table 2). No macrofauna were found in 0.2 mm mesh bags. Weight losses from 1.0 mm mesh bags, which were colonised by macrofauna, were not significantly different as determined by analysis of covariance from weight losses from 0.2 mm mesh bags (see also Fig. 2); thus macrofauna colonising the bags did not affect weight losses from the enclosed litter. Weight losses therefore can be dominantly attributed to the combined affects of leaching and microbial metabolism. Losses resulting from abrasion were probably small since litter was enclosed in bags.

Although animal feeding was unimportant in the litter bag experiment it undoubtedly occurs in the stream itself. Larvae of *Z. ingens* and *A. cyrene* in Middle Bush stream are known to feed primarily, If not exclusively, on beech leaves and have been estimated to consume from 62-124 g/m^2 annually (Winterbourn and Davis, 1976). This contradiction emphasises a major limitation of the litter bag method. If large mesh sizes are used the natural conditions under which litter normally exists in a stream are more nearly realised but an uncontrolled loss of fine particles may occur, resulting in an overestimation of weight losses. On the other hand if retention of fine particles is optimised by using smaller mesh sizes, free passage of macrofauna is restricted and estimates of weight loss will not assess the effect of their feeding activities.

TABLE 2. *Mean numbers of larger litter processing macroinvertebrates collected from litter bags.*

Taxon	Mean numbers per bag	
	Present study (Jul 1973-Aug 1974)	Davis and Winterbourn (1971) (Nov 1974-Mar 1975)
Trichoptera		
Zelandopsyche ingens	0.4	0.9
Olinga jeanae	0.8	0.4
Plecoptera		
Austroperla cyrene	0.2	0.2
Coleoptera		
Helodidae	0.9	1.0

3. *Mechanisms of weight loss*

Several models have been used to describe weight losses from stream litter. The simplest assumes a constant rate of loss. The accumulated loss (L) after time t is described by

$$L = a + kt \qquad (1)$$

where a is a constant approximating initial weight loss resulting from rapid leaching and k is the loss rate coefficient. This model is not usually defined by authors but is implicit in the assumption of linearity of weight loss (e.g., Davis and Winterbourn, 1977).

A negative exponential model also has been used to describe litter disappearance in streams (Petersen and Cummins, 1974; Sedell, Triska and Triska, 1975; Triska and Sedell, 1976). This model assumes a constant fractional loss of weight. The proportion of initial weight remaining (R) after time t is described by

$$R = a.e.^{-kt} \qquad (2)$$

and the accumulated weight loss after time t may be calculated by

$$L = 1 - a.e^{-kt} \qquad (3)$$

Least squares regression analyses of weight loss data obtained in the present study gave significant fits to both models described above; however, coefficients of determination (r^2) indicated that weight losses were better described by a positive exponential model (Table 3). This model assumes an increasing fractional loss of weight. The accumulated weight loss after time t is described by

$$L = a.e^{kt} \qquad (4)$$

It should be emphasised that equations 3 and 4 describe fundamentally different models of weight loss. A negative exponential model describes a decreasing rate of weight loss with respect to initial weight, whereas a positive exponential model describes an increasing rate of loss.

A negative exponential model of weight loss from decomposing litter assumes a constant proportion of decomposer enzyme per unit of litter substrate (Saunders, 1976). This enzyme is usually attributed to microflora - particularly aquatic hyphomycetes- colonising litter (Iversen, 1973; Cummins, 1974: Suberkrop and Klug, 1974; Willoughby, 1974). Cummins (1974) suggested that most microbial colonisation takes place during the first few weeks of immersion and Suberkrop and Klug (1976) have

TABLE 3. *Least squares regression equations for three models of weight loss from mountain beech litter.*

Model	Equation	F-ratio	r^2
Linear	$\%L = - 2.628 + 0.149.t$	528*	0.89
Negative exponential	$\%L = 100 - (108.203.e^{-0.002.t})$	299*	0.83
Positive exponential	$\%L = 4.554.e^{0.008.t}$	631*	0.91

$* = p < 0.01$.

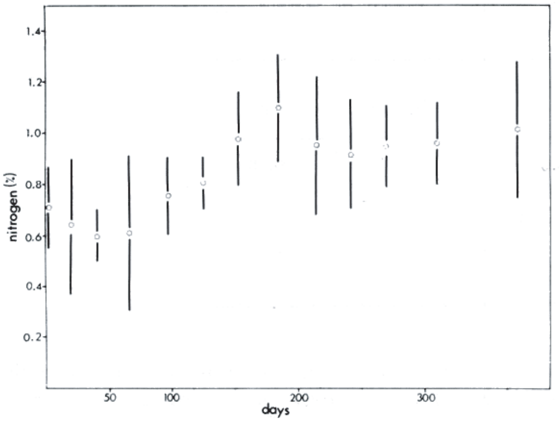

FIGURE 3. *Nitgrogen contents of mountain beech litter kept in mesh bags in the stream. Vertical bars indicate 95% confidence limits of the mean.*

shown A TP concentrations in submerged hickory and oak leaves to reach maximum levels after about two weeks. Increases of nitrogen concentration in decomposing litter have been recorded by several workers (e.g., Iversen, 1973; Triska, Sedell and Buckley, 1975) and are attributed to colonisation by microflora. Concentrations usually reach a maximum after the first 30-60 days and thereafter remain at relatively constant levels. Subsequent to maximum colonisation, the activity of microflora on stream litter decreases markedly, probably because the more easily metabolised components of the litter become exhausted (Saunders, 1976). Weight losses from litter in streams therefore may be expected to take place most rapidly during the early part of the decomposition process when microbial populations are high. Thereafter, as labile components of litter become limiting, rates of microbial utilisation should fall, resulting in a declining rate of weight loss. This mechanism of weight loss may be characterised by a negative exponential curve (Fig. 4c).

If, on the other hand, microbial colonisation of litter takes place slowly and populations are increasing during much of the residence time of litter in a stream, decomposer enzyme concentrations per unit of litter substrate should continue to increase for some time. This should result in an increasing rate of weight loss from litter. In the present study percentage nitrogen concentrations recorded from decomposing mountain beech litter, which were attributed to bacterial colonisation (Davis and Winterbourn, 1977), did not reach maximum levels until after 190 days (Fig. 3). This suggests that microbial colonisation of mountain beech litter occurs at a slow rate and provides an explanation for the increasing rate of weight loss (see Fig. 4a). This mechanism of weight loss may be characterised by a positive exponential curve.

Rates of decay, however, cannot continue to increase indefinitely. The exhaustion of labile components of the litter (and other limiting factors) inevitably will slow rates of litter breakdown by microflora. At some point during the decomposition process microbial populations should reach a maximum standing crop and subsequent enzyme concentrations would remain constant. Weight loss rates should then decline. In fact, in the present study after 372 days, weight losses from mountain beech litter fell well below those predicted by the positive exponential model (see Fig. 4). At this time microbial utilisation of the litter may well have been limited, resulting in an inflexion of the curve describing weight losses towards a decreasing rate of loss. This kind of curve, which incorporates both an increasing and a decreasing weight loss phase, is predicted by a logistic model and accumulated weight loss after time t is described by

$$L = \frac{a}{1 + e^{b-ct}}$$

where a is the asymptotic value for weight loss and band c are loss rate coefficients. This model was fitted to weight loss data for mountain beech litter using an iterative algorithm (MQUADT; Conway, Glass and Wilcox, 1970). Fitted parameter values are shown in Table 4. This model provides a better explanation of the variance in weight losses than any of the previously fitted models (see Fig. 4).

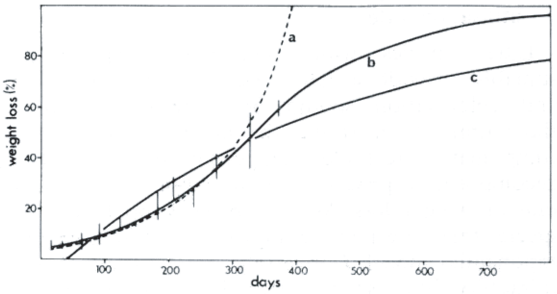

FIGURE 4. *A comparison of three models describing weight losses from mountain beech litter kept in mesh bags in the stream.* a) *positive exponential model;* b) *logistic model;* c) *negative exponential model.* a *and* c *fitted by least squares regression,* b *fitted using MQUADT algorithm. Vertical bars represent the range of measured weight losses. Note-curves extrapolated from 372 days.*

TABLE 4. *MQUADT fitted parameters for a logistic model of weight loss from mountain beech litter (equation* 5 *in text).*

Parameter	Parameter value	Confidence limits (95 %)	F-ratio	r^2
a	97.1	90.6 - 103.6	2706*	0.98
b	3.08	2.97 - 3.20		
	-0.010	– 0.900 - –0.009		

* = $p < 0.01$.

Although decomposition of stream litter is a continuous process it is possible to separate it into two distinct phases since different mechanisms are identifiable at different times. To summarise, these are:

1. Rapid weight loss through leaching of water soluble components. This is usually completed within a few days of immersion and the mechanisms controlling it are largely, if not entirely, physico-chemical.
2. A phase of relatively slow weight loss, primarily mediated by biological mechanisms. This phase may be further separated into two components characterised by different rates of weight loss. (a) an initial component during which weight loss rates increase as a result of microbial colonisation and utilisation of the litter substrate. (b) a second component during which weight loss rates decline. This results from micro-environmental factors which prevent further microbial population growth 'and therefore limit utilisation rates.

Litter species which decompose rapidly presumably provide a labile substrate for microflora and colonisation should be completed within a short time. As a result, the increasing weight loss component is restricted temporally and most of the decomposition process should exhibit a decreasing rate of weight loss. Weight losses from labile litter species therefore may be approximated by a negative exponential model. Conversely, colonisation of more refractory litter species should be slower and the period during which weight loss rates are increasing may be extended temporally. Weight losses from refractory litter species, which decompose slowly, therefore may be approximated by a positive exponential model, at least during the period over which most decomposition studies have followed weight loss (i.e. about one year).

Because decomposition is a continuous process, weight losses described by positive and negative exponential models may be interpreted as different parts of the same curve. Each is accommodated by an "S-shaped" curve by shifting the point of inflexion between the positive and negative rate phases; closer to the origin for labile litter species which decompose rapidly and further away from the origin for refractory litter species which decompose slowly.

Clearly, this provides only a simplistic view of litter decomposition in streams. Perhaps the major weakness of the logistic model (in common with all other simple models) is that rates of microbial colonisation of litter are not necessarily a function of time alone. Temperature, pH, stream discharge and the physical condition of pre-immersion litter may influence colonisation rates (Triska, 1970), and factors other than microbial utilisation may be instrumental in influencing weight losses from stream litter. Probably, the most significant additional variable results from the feeding activities of aquatic macroinvertebrates.

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